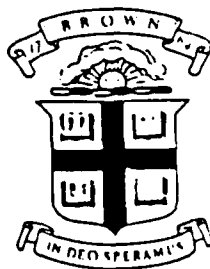


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Technical Report

CLUTTER INTERFERENCE AND THE INTEGRATION TIME OF ECHOES IN THE
ECHOLOCATING BAT, EPTESICUS FUSCUS

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19 ABSTRACT (Continue on reverse if necessary and identify by block number) The ability of the echolocating bat, <i>Eptesicus fuscus</i> , to detect a sonar target is affected by the presence of other targets along the same axis at slightly different ranges. If echoes from one target arrive at about the same delay as echoes from another target, clutter interference occurs and one set of echoes masks the other. Although the bat's sonar emissions and the echoes themselves are 2 to 5 msec long, echoes (of approximately equal sensation levels--around 15 db SL) only interfere with each other if they arrive within 200 to 400 msec of the same arrival-time. This figure is an estimate of the integration time of the bat's sonar receiver for echoes. The fine structure of the clutter-interference data reflects the reinforcement and cancellation of echoes according to their time separation. When clutter interference first occurs, the waveforms of echoes already overlap for much of their duration. The masking effect underlying clutter interference appears specifically due to overlap (OVER)					
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not between raw echo waveforms, but between the patterns of mechanical excitation created when echoes pass through band-pass filters equivalent to auditory-nerve tuning curves. While the time scale of clutter interference is substantially shorter than the duration of echo waveforms, it still is much longer than the eventual width of a target's range-axis image expressed in terms of echo delay. The image presumably is produced after several stages of processing, and clutter interference evidently involves interactions occurring at an intermediate stage.

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Abstract

The ability of the echolocating bat, *Eptesicus fuscus*, to detect a sonar target is affected by the the presence of other targets along the same axis at slightly different ranges. If echoes from one target arrive at about the same delay as echoes from another target, clutter interference occurs and one set of echoes masks the other. Although the bat's sonar emissions and the echoes themselves are 2 to 5 msec long, echoes (of approximately equal sensation levels--around 15 dB SL) only interfere with each other if they arrive within 200 to 400 μ sec of the same arrival-time. This figure is an estimate of the integration time of the bat's sonar receiver for echoes. The fine structure of the clutter-interference data reflects the reinforcement and cancellation of echoes according to their time separation. When clutter interference first occurs, the waveforms of echoes already overlap for much of their duration. The masking effect underlying clutter interference appears specifically due to overlap, not between raw echo waveforms, but between the patterns of mechanical excitation created when echoes pass through band-pass filters equivalent to auditory-nerve tuning curves. While the time scale of clutter interference is substantially shorter than the duration of echo waveforms, it still is much longer than the eventual width of a target's range-axis image expressed in terms of echo delay. The image presumably is produced after several stages of processing, and clutter interference evidently involves interactions occurring at an intermediate stage.

INTRODUCTION

Echolocating bats emit sonar sounds and perceive objects from the echoes of these sounds that reflect back to their ears (Busnel and Fish, 1980; Griffin, 1958; Nachtigall, 1988). Echolocation is an acoustic-imaging process that yields spatial images for guiding the bat's flight and pursuit of prey (Simmons, 1987; Simmons and Stein, 1980). The big brown bat, *Eptesicus fuscus*, is one of many insectivorous species of bats that feed upon flying insects which they find using sonar. The sonar signals emitted by *Eptesicus* are frequency-modulated (FM) sounds that range in duration from about 0.5 to 15 msec, depending upon the activity of the bat--the stage of pursuit, for example (Griffin, 1958; Kick and Simmons, 1984; see Fig. 2 in Simmons, 1987). During the approach to a target, each sound sweeps downward in frequency in two strong harmonics from about 55 to 25 kHz and from 110 to 50 kHz. Other species that produce a broadly similar pattern of emissions during pursuit include *Pipistrellus kuhli* and *Tadarida brasiliensis* (Schnitzler, et al., 1987; Simmons, et al., 1978). The rate of sweep in these FM signals is such that they cover on the average a span of 1 kHz in only a few hundred microseconds, and the shortest sounds emitted near the end of an interception maneuver (in the terminal stage) sweep through this range in even less time. The rapid passage of the FM sweep through any given frequency region limits the nature of the auditory representation of FM echoes.

The auditory mechanisms of echolocation--in particular, the processing of FM echoes for information about target range--have been studied through neurophysiological experiments with the

mustached bat, *Pteronotus parnellii*, a species that emits constant frequency (CF) signals coupled to its FM signals (Suga, 1988), as well as with several species that emit predominantly FM sounds, such as the little brown bat, *Myotis lucifugus* (Suga, 1970; Sullivan, 1982; Wong and Shanon, 1988), the Mexican free-tailed bat, *Tadarida brasiliensis* (Bodenhamer and Pollak, 1981; Pollak, *et al.*, 1977), and *Eptesicus fuscus* (Feng, *et al.*, 1978). A composite description of the initial auditory encoding of the time-of-occurrence of FM echoes can be assembled with the data collected from these species (Simmons and Kick, 1984). Bats receive both FM their sonar emissions and echoes through the inner ear (Kawasaki, *et al.*, 1988), which filters incoming sounds through numerous, parallel, overlapping band-pass filters whose frequency responses correspond roughly to the tuning curves of primary auditory neurons. Each FM sonar sound or echo appears to the band-pass filters of the bat's auditory-nerve fibers to consist of a succession of short bursts of sound (in the limiting case, impulses) whose center frequencies correspond approximately to the characteristic frequency of the tuning curves for the neurons. The dwell-time of the FM signal within the excitatory response area for each cell is therefore brief, and the auditory nervous system thus must base a substantial amount of its image-processing on the time-of-occurrence of events within each frequency channel (Simmons, 1980).

When the FM sweep of a sonar emission or an echo enters the tuning curve of an auditory neuron in an "FM" bat, it evokes an initial or *on*-discharge that registers the time-of-occurrence of the fiber's excitatory frequency with surprising sharpness both in

time and in frequency (Bodenhamer and Pollak, 1981). Depending upon the amplitude of the sound, it then may evoke several additional discharges that, however, are not as sharply coupled to the time-of-occurrence of the excitatory frequency as the on-discharge. At higher levels of the bat's auditory system, these on-discharges are preserved, while the secondary discharges are deleted from the response profiles of many neurons. In FM bats, across a large population of auditory neurons in the inferior colliculus whose characteristic frequencies are encompassed by the FM sweep, the FM signal is represented as the neural equivalent of a spectrogram by these on-discharges (Altes, 1980, 1981; Simmons, 1973; Suga, 1972). The instantaneous frequency of the sound is conveyed into the auditory system by the on-discharge in each of the differently-tuned fibers of the auditory nerve. Both the bat's own emitted sounds (which stimulate the bat's ears directly through the air from the mouth) and their echoes are represented by spectrogram-like arrays of nerve discharges (Simmons and Kick, 1984). Such a mixed time/frequency format places great emphasis on the capacity of the bat's auditory system to keep track of the timing of each frequency (the momentary value of instantaneous frequency) in emissions and in echoes. The experiment reported here focuses on limitations that this spectrogram format creates for the detection of discrete targets by the bat.

In sonar, *Clutter interference* occurs when the presence of one target masks the presence of another. It is commonly described in terms of competition between the echoes from one target and echoes from the other target within the sonar receiver (Skolnik, 1962).

Eptesicus experiences clutter interference when two targets fall closer together than 8 to 9 cm along the range axis (Simmons, et al., 1988). The masking effect that constitutes clutter interference presumably occurs because the representation of echoes from one target merges with the representation of echoes from the other target to render them indistinguishable. In *Eptesicus*, this evidently happens when echoes come nearer to each other than about 0.5 msec in delay. The neural representation of echoes changes as one ascends the auditory system (Simmons, 1987; Suga, 1974, 1984), but from the auditory nerve to the inferior colliculus it essentially takes the form of a spectrogram. If two echoes, each of which evokes a spectrogram-like array of nerve discharges, become sufficiently close together in time, their spectrograms will collide and the discharges that make them up will mingle together to form a compound representation (see Beuter, 1980). If the occurrence of a discrete spectrogram-like array of neural discharges does indeed represent each echo, the width of the clutter-interference zone along the range axis ought to be related to the width along the time axis of the time-frequency "cells" that make up the spectrogram. The experiment reported here was undertaken to determine whether clutter interference in echolocation occurs because spectrogram-like auditory representations of two echoes overlap and can no longer be distinguished as separate. The approach was to measure the strength of clutter interference for various time-separations between two echoes of approximately equal sensation levels and to compare the results with a simple model of

the peripheral auditory interactions that would occur when two echoes overlap each other in time.

METHODS

The animals used in these experiments were five big brown bats, *Eptesicus fuscus* (family Vespertilionidae), obtained from the attics of houses in the vicinity of Providence, Rhode Island. Each bat was trained in a two-alternative forced-choice procedure to detect an electronically reproduced *test echo* of its own sonar sounds arriving at a delay of 3.27 msec, which corresponds to a target at a range of about 56.5 cm. (The delay of an echo is composed of the outgoing and return travel times, for a total of 58 μ sec for each centimeter of range.) Additional echoes, which served as *clutter echoes*, were presented at variable delays around that of the test echo, and their effects upon detection performance were measured to determine the shape of the clutter interference zone surrounding each echo along the delay (range) axis.

Target simulation: The procedure for training bats and conducting clutter interference experiments is described in detail elsewhere (Simmons, et al., 1988). It is summarized here with reference to the particular procedure used in the present experiment. Fig. 1 shows schematically the design of the experiment and the method used to present

INSERT FIG. 1 ABOUT HERE

the bat with electronically-reproduced echoes that simulate sonar targets at different distances. The bat was trained to sit on an elevated, Y-shaped platform and broadcast its sonar sounds to the front--somewhat to the left and the right--to detect a *test target* (*a* in Fig. 1) presented in association with two *cluttering targets* (*b₁* and *b₂*). It was rewarded with a piece of a mealworm offered in forceps for each correct response (arrow), which consisted of crawling forward onto the left or right arm of the platform--whichever was in the direction of the test target being presented on that particular trial. The appearance of the simulated test target on the left or right was determined by a pseudorandom schedule and set by a switch located beneath the platform. The experiment was set up in a 4.5 x 3.5 x 2.4 meter chamber lined on walls, ceiling, and floor with convoluted polyurethane foam (Permafoam Corp.) that reduced the amplitude of ultrasonic reverberation by at least 20 to 30 dB compared with what would occur if the chamber had smooth, hard walls.

The electronic system for simulating sonar targets was built around the bat's observing position on the Y-shaped platform. Two Bruel & Kjaer Model 4138 condenser microphones (*m* in Fig. 1) were mounted at the ends of the arms of the platform to pick up the bat's echolocation sounds. The electrical signal from each microphone was amplified, filtered to a 20 to 100 kHz band with a Rockland Model 442 band-pass filter, delayed by a controlled amount, and then returned to the bat from an RCA electrostatic loudspeaker (Part No. 112343; *s* in Fig. 1) that was mounted next to the microphone. The signals recorded from the bats were stored on

analog magnetic tape with a Racal Store-4 tape recorder and subsequently reproduced for analysis in an IBM PC-AT computer operating with ILS programs from Signal Technology, Inc. Both the microphones and the loudspeakers were located 20 cm from the bat's observing position at the center of the platform, so that together they provided a propagation delay of 1.16 msec for any sound emitted by the bat and returning to the bat's ears. The angle separating the two sets of microphones and speakers was approximately 40°.

On a given day of the experiment, each bat was run on a number of trials that was determined by its current body weight and the quantity of mealworms consumed after correct trials. Each day's run constituted a block of trials for one experimental condition, and the stimuli were set to a new condition on the following day. The bats typically worked through 25 to 50 trials in each block. If the number of trials achieved on a single day was less than this, the same stimulus conditions were repeated the next day to accumulate more trials. The bats in this experiment were run by different experimenters who were not given information about the form likely to be taken by simultaneous and near-simultaneous masking effects with broadband stimuli.

During each experimental trial, which lasted for several seconds, the bat emitted sounds with durations of 2 to 5 msec at rates of 5 to 15 sounds per second (see below). Each sound was received at both microphones, with an amplitude at each microphone that depended on the aim of the bat's head during head-scanning movements as the bat searched for the target (Simmons and Vernon, 1971). The amplified and filtered signal representing each of the

bat's sonar sounds was delayed electronically by a digital delay system (*delay* in Fig. 2) designed and built by the Science Services Shops at the University of Oregon (Simmons, *et al.*, 1988). The signal was digitized with up to 12-bit accuracy at a rate of 750 kHz, stored in a circulating buffer memory, and then read out and reconstituted as an analog signal after a preset delay. The electronic delay was chosen so that, when added to the 1.16-msec propagation delay from the bat to the microphone and from the loudspeaker to the bat, it created a total delay corresponding to the desired simulated target range. Each microphone-loudspeaker channel was equipped with a delay system, so the bat could be presented with simulated targets that appeared on the bat's right and on its left from the observing position on the platform.

The amplitude of the sounds picked up by the microphones varied by about 6 to 8 dB as the bat moved its head to the left and right while scanning the simulated targets, and the gain of the circuits feeding into the delay lines was set to use all 12 bits of the analog-to-digital converter's range for the strongest of these sounds. The noisiest electronic component in each simulator channel was the microphone, specifically the first stage of its preamplifier, and the noise from this source determined the signal-to-noise ratio of the echoes eventually delivered back to the bat. The RMS amplitude of this noise was about 30 to 35 dB lower than the peak-to-peak amplitude of most of the signals picked up from the bat. When the bat moved its head, the signal-to-noise ratio of echoes changed slightly because the internal noise of the microphones remained constant while the signals recorded from the

bat fluctuated in amplitude. Each bat generally broadcast its sounds directly at both the left and right channels before making its choice, which maximized the strength of the signals with respect to the noise. The bat thus kept the effective signal-to-noise ratio of most echoes relatively stable even though it moved its head during the course of experimental trials.

The test echo (*a* in Fig. 1) was simulated on either the left or the right channel with a propagation delay of 1.16 msec added to an electronic delay of 2.115 msec to create an overall delay of 3.27 msec. This is the echo that the bat was trained to detect. In addition, cluttering echoes (*b*₁ and *b*₂ in Fig. 2) were simulated on both the left and the right channels regardless of which channel was delivering the test echo. Both cluttering echoes appeared at the same delay on any one trial. The delay of the cluttering echoes was varied in stages from being greater than the test-echo delay to being less than the test-echo delay to map out the zone of clutter interference that surrounded the test echo (Simmons, et al., 1988). The longest simulated range for the two cluttering targets was 185.5 cm, created by adding an electronic delay of 9.602 msec to the propagation delay of 1.16 msec. The shortest simulated range was 25.6 cm, created with a 0.325-msec electronic delay added to the propagation delay.

Clutter interference: For each bat, the experiment consisted of two parts in terms of the movements of the cluttering targets. In the first part, the cluttering targets began at a simulated distance of 185.5 cm and moved nearer to the bat on successive blocks of trials until they eventually were at a distance of 25.6

cm. They were moved nearer in steps of about 5 or 10 centimeters until they had passed the location of the test target at 56.5 cm and became closer than it was to the bat. In this first part, the clutter interference zone was sketched in rather coarsely by the 5 to 10 cm steps. In the second part of the experiment, the cluttering targets began at a simulated range of 58.5 cm and moved nearer on each block of trials in smaller steps of about 1 cm or even less until they had passed the test target and came to a range of 54.3 cm. In this finer-grained measurement of the clutter interference zone in the immediate neighborhood of the test target, the fine structure of the zone was determined.

Acoustic calibration: The target simulator is an acoustic recording and reproducing system whose performance can be summarized by a frequency-response curve or transfer function. The frequency response of the left and right channels of the simulator is shown in Fig. 2. These curves

INSERT FIG. 2 ABOUT HERE

refer to the ratio of the acoustic output of the system measured at the bat's observing position relative to the acoustic input delivered to a point 20 cm in front of the bat--that is, at the location of the microphone. The attenuators internal to the simulator were set to zero (maximum system gain) for these frequency-response measurements. In the experiments themselves, the electronic attenuation of echoes by the simulator was in the range of 17 to 24 dB

depending on the individual bat (see below). Calibration of the simulator's microphone-to-loudspeaker path was accomplished by replacing the bat with a third loudspeaker and microphone to broadcast sounds of known characteristics into the system and record the output returned to the bat's observing position. This was done by placing an uncovered Bruel & Kjaer Model 4135 condenser microphone at the bat's location and broadcasting 1-msec FM signals (10 to 100 kHz) into the system from a specially-built electrostatic loudspeaker that could generate sounds comparable in strength to the bat's emissions (Simmons, *et al.*, 1979).

The simulator's overall performance was monitored daily by an automatic calibration system built into the target simulator to detect any malfunction of the simulator's acoustic or electronic components. In December 1986, at the start of the experiment, an input of 100 dB SPL peak-to-peak at 40 kHz would produce an echo of 90 dB SPL peak-to-peak at maximum (0 dB) gain, and twelve months later, after the experiment was over, an input of 100 dB SPL would produce an echo of 87 dB SPL. The simulator was adjusted daily to maintain its zero dB gain within this 3 dB span for all experimental trials.

The amplitudes of the test echoes delivered to the bats were set to a fixed level with respect to each bat's threshold for detecting the test target presented in isolation. That is, the test echo was always of the same sensation level to the bat. To determine the specific threshold for each bat prior to the beginning of the experiment, the amplitude of the test echo was reduced from about 80 dB SPL peak-to-peak in steps of 5, 2, or 1 dB

on successive blocks of trials to find the level at which the bat's performance in the two-choice detection task declined below 75 percent correct responses, which was taken to be the threshold. No cluttering echoes were presented during this procedure. The test echo was then set to a value 15 dB above the bat's threshold (15 dB sensation level, or SL) throughout the rest of the clutter experiment. The cluttering echoes were also set to a fixed amplitude of 15 dB SL when they appeared at the same delay as the test echo. At other delays, they had to be adjusted in amplitude because the threshold for echo detection in *Eptesicus* depends upon target range or echo delay (Kick and Simmons, 1984). The correction amounted to 11 dB for each doubling of range or delay, apportioned logarithmically over the span from 25.6 cm to 185.5 cm in 1-dB steps. As a result, cluttering echoes simulated to arrive from further away than the test target were weaker than the test echo in sound pressure units, but the bat's threshold for echo detection is lower at greater ranges, so the sensation level was kept approximately constant. The cluttering echoes were at the same sound pressure as the test echo when they appeared at the same range, and they were stronger when they appeared nearer than the test echo.

RESULTS

The initial step in the experiment was measurement of each bat's threshold for detecting the isolated test echo. The threshold levels obtained for the five bats that subsequently finished all or part of the experiment were 48 dB SPL peak-to-peak (Bat 1), 55 dB SPL (Bat 2), 55 dB SPL (Bat 3), 51 dB SPL (Bat 4), and 54 dB SPL (Bat 5). The threshold for echo detection at a delay of about

3 msec by *Eptesicus* normally is near 20 dB SPL peak-to-peak (Kick and Simmons, 1984). This normal threshold is measured in an apparatus with only small microphones located near the bat; the loudspeakers are placed much farther away to avoid interference from what would be their relatively strong echoing surfaces if they were placed close to the bat. However, such an arrangement is not sufficiently flexible for interference experiments that require the return of multiple echoes over a wide span of delays. Both the microphones and the loudspeakers have to be located near the bat to create the test and the cluttering echoes together. In the target simulator used here, they are only 20 cm away. The RCA loudspeakers were used here as a compromise because they are relatively small and thus reflect weaker incidental echoes than larger loudspeakers which might have a slightly flatter frequency response (see Fig. 2).

The left and right arms of the platform extend 10 cm away from the bat, leaving a gap of 10 cm past the end of the platform to keep the bat from biting the microphones or the loudspeakers. (The bat receives its reward from forceps after it has moved to the end of the platform, and it occasionally mistakes the microphone or the speaker for the food.) While the loudspeakers are relatively small, they still reflect a substantial echo from 20 cm away that elevates the bat's echo-detection threshold for the test echo which arrives about 2 msec later. When the microphones and speakers are moved nearer, to a distance of only 10 cm, where their supports are entirely hidden below the edges of the arms of the platform, the echo they reflect falls considerably in amplitude and the bat's

echo detection threshold drops back down to the region of 20 dB SPL (Kick and Simmons, 1984; Simmons, *et al.*, 1988). The experiment to measure the clutter interference zone lasted many months and gave the five bats numerous opportunities to damage the expensive microphones in the simulator. Consequently, the microphones were kept 20 cm from the bat even though the bat experienced an elevated threshold as a result.

After determination of the echo detection threshold, five bats finished the clutter interference experiment to varying degrees. Fig. 3 shows the individual performance of all five bats (percentage correct responses) in the clutter interference experiment, and Fig. 4 shows their mean

INSERT FIGS. 3 AND 4 ABOUT HERE

performance. All five bats completed at least part of the experiment, and two bats completed all conditions, including both the coarse and fine-grain mapping of the clutter interference zone. In Fig. 3a, three bats are represented in the data for clutter delays smaller than the delay of the test echo (3.27 msec), and five bats are represented in the data for delays larger than the delay of the test echo. In the region very close to the test echo delay, where the curve shows pronounced fine structure (Fig. 3b), four bats are represented in the data. The coarse shape of the clutter interference zone can be summarized by its width at a performance level of 75 percent correct responses. In Fig. 4, the average curve extends about 400 μ sec earlier than the test echo and about 300 to 500 μ sec

later. In terms of simulated target range, the clutter interference zone thus extends about 7 cm along the range axis on either side of the test target at a range of 56.5 cm. The strength of the interference produced by the cluttering echoes depends upon where they fall with respect to the test echo. When the delay of the cluttering echoes is close to the delay of the test echo, the bats experience pronounced masking in their attempts to detect the test target. When the delay of the cluttering echoes is more remote from the test echo's delay, masking is reduced or absent.

The degree of masking experienced by the bats fluctuates greatly as a function of the position of the cluttering echoes with respect to the test echo when they fall within about 100 μ sec of each other. These fluctuations show up poorly in plots of the entire clutter interference zone owing to the compressed time scale of the graphs in milliseconds. Fig. 3b shows the central region of the clutter interference zone for the individual bats, and the inset to Fig. 4 shows the central region for the mean data of four bats. The time scale has been expanded to only a few hundred microseconds. This "fine structure" in the clutter zone is found in the data for all of the bats. It is a consequence of temporal overlap of the test and cluttering echoes and represents the mutual interference (reinforcement and cancellation) of their waveforms (see below).

The sonar signals emitted by all five bats during detection trials in the clutter interference experiment are quite similar to each other. Over the five bats, the sounds are about 2 to 5 msec in duration, with the vast majority in the range of 2.5 to 4 msec,

with a modal duration of about 3.5 msec. The signals have an FM harmonic structure that is typical of signals used by *Eptesicus fuscus* (see Fig. 2 in Simmons, 1987, for example). Fig. 5 shows spectrograms of six sample signals recorded from each bat during the choice period from representative trials.

INSERT FIG. 5 ABOUT HERE

Some bats made sounds that were consistently longer than other bats (Fig. 5D compared to Fig. 5E, for example), but there is variability of only a millisecond or two in the durations used by any one bat. The detailed differences among the signals shown in Fig. 5 are usually found in *Eptesicus*. Much of the variability in the appearance of the spectrograms is correlated with the variability in the duration of the sounds. Shorter signals generally have a stronger third harmonic around 90 kHz than do longer signals (compare the six signals in Fig. 5D with each other, for example). The bats worked entirely within their normal repertoire of echolocation signals when they performed the detection task in the presence of clutter.

DISCUSSION

This experiment was undertaken specifically to measure the shape of the clutter interference zone for test and cluttering echoes of equal strength, using an experimental procedure that keeps the test echo and the cluttering echo from the same loudspeaker in tight temporal registration with the sonar emission that precedes them. No matter how much the bat moves its head during

experimental trials, the test echo and the cluttering echo from the same channel of the target simulator will always be separated by the time interval set on the switches of the electronic delay line. In previous clutter interference experiments with *Eptesicus*, two factors disrupted the tight temporal registration of the test and cluttering echoes, causing their results to miss the fine structure in the clutter interference zone. In one experiment (Simmons, et al., 1988), real targets were used to generate the cluttering echoes, while the test echoes were simulated electronically. Because the microphones and loudspeakers involved in returning the test echoes were in physically different locations than the targets producing the clutter, the bat's head movements when they scanned the targets during trials had different effects on the path-length traveled by the test echoes compared to the cluttering echoes. The bat's head movements were equivalent to shifting the test and cluttering targets along the range axis by small amounts, thus breaking their correlation with each other. In a second experiment (Simmons, et al., 1988), the test and cluttering echoes all were simulated electronically, as they were here, but the signals from the two microphones were mixed to create a composite "emission" that was then returned at appropriate delays by electronic means. Once again, the bat's head movements disrupted the coupling of test and cluttering echoes on the fine scale of microseconds. In both of these earlier experiments, the overall shape of the clutter interference zone was traced by the results, but the fine structure occurring as a consequence of reinforcement and cancellation of

echo waveforms was washed out by the lack of tight registration of their delays.

In the experiment reported here, the amplitude of the echoes used as stimuli was adjusted to keep them approximately at a fixed sensation level of 15 dB to remove from the data most of the extraneous distortions of the shape of the clutter interference zone that might be caused by delay-related changes in the bat's threshold of hearing (Kick and Simmons, 1984). The shape of the clutter interference zone measured in this way is an important piece of information about the bat's sonar receiver--it is the silhouette of the auditory system's most limiting representation of the waveform of an echo, cast as a shadow along the delay or range axis.

The effects of clutter interference reveal the conditions under which two echoes merge into one, at least as far as a simple detection task is concerned. Measurements of the strength of masking at different time separations of the test and cluttering echoes indicate the point at which the underlying representations of echoes first run against each other. From the average curve in Fig. 4, the bats' performance first appears to drop from a normal level above 85 to 90 percent correct responses at time separations about 1 msec removed from the arrival-time of the test echo. At 75 percent correct responses, the effects of clutter interference extend over a span of about 300 to 400 μ sec around the arrival-time of the test echo. These results are in close agreement with the results of previous experiments on clutter interference (Simmons, *et al.*, 1988) and in general agreement with observations on the

effects of clutter during airborne interceptions (Webster, 1967; Webster and Brazier, 1965). Some trace of the representation of echoes at the amplitude used here must linger as long as 300 μ sec to 1 msec after the nominal arrival-time of the sound to create the interference observed here. The trace is not constant in strength but diminishes rapidly beginning at about 200 μ sec, however. This trace can combine with the representation of other echoes to obscure their presence. At some level of the auditory system, the traces of two echoes must, in effect, merge if they arrive closer together than 300 μ sec to 1 msec in delay.

As observed in previous experiments, the sonar sounds themselves are several times longer than the clutter interference interval, indicating that clutter interference is not a consequence of temporal overlap of the raw waveform of echoes but rather temporal overlap of a representation of these waveforms that is inherently more compressed along the time axis than the sound-pressure waveform itself (Simmons, *et al.*, 1988). In the present experiment, the sonar sounds emitted by the bats were 2 to 5 msec long (Fig. 5), but the clutter interference effect already is greatly diminished for echo separations of only half a millisecond (Fig. 4). For purposes of interference, then, the effective duration of each echo is roughly ten times shorter than the echo itself.

Sounds received by the ear are changed in amplitude and relatively gently filtered until they reach the inner ear, where they undergo the first radical change associated with auditory signal-processing. The Organ of Corti distributes different frequencies

of sound to different regions along the basilar membrane, in the process effectively passing the sound through a bank of parallel, overlapping band-pass filters. The basilar membrane breaks the FM sweeps of sonar emissions and echoes into overlapping segments whose center frequencies and bandwidths correspond to the frequency response of the band-pass filters. These segments of the FM waveform represent mechanical excitation delivered to individual inner hair cells along the basilar membrane. The same segmentation occurs in time as well as frequency because the frequencies of the signals appear in succession and the filters have finite impulse responses. The rate-of-sweep of the sounds and the sharpness of filter tuning are such that the segments of the FM sweep are only a few hundred microseconds long (see Beuter, 1980), which is similar to the size of the clutter interference zone. If two echoes are close enough together that the bursts of mechanical excitation they evoke become mixed, separate detection of the two echoes could be difficult to achieve.

The acoustic basis for detecting test echoes in clutter: In the clutter interference experiment, the bat has to detect the the test echo in the presence of clattering echoes that overlap with it to varying degrees. The specific stimuli for the bat's correct choice consist of pairs of echoes placed along the axis of delay according to the horizontal axis of Fig. 3 or Fig. 4. The individual echoes in each pair sum together to create a pattern of interference that affects both the waveform itself and its spectrum. Fig. 6 shows the waveforms of a series of echoes formed by overlap of two replicas of an *Eptesicus* sonar signal separated by

INSERT FIG. 6 ABOUT HERE

different intervals of time (Δt). These echoes represent what is reflected by two reflecting points, or glints, separated by different distances along the range axis. Here, one glint is the test target and the other glint is the clutter. The bat's emission in this instance is 2.5 msec long, with a multiple-harmonic, FM composition similar to that of the sounds shown in Fig. 5. In the case of zero time separation (upper left of Fig. 6), the echo consists of two replicas of the emission superimposed at the same time; it thus has a waveform identical to the emission. As the amount of time separation increases, the waveforms of the two components of the whole echo reinforce and cancel each other in a manner that depends upon their frequencies and bandwidths. For large time separations (600 μ sec; lower right of Fig. 6), the components are far enough apart that they only partially overlap and begin to be distinct within the waveform as a whole. The overlapping portion has rapid amplitude modulations caused by interference. If the separation were to approach the duration of the bat's signal, the two components would become totally separate acoustic events.

In the waveforms in Fig. 6, the immediate manifestation of the interference between components changes as the time separation increases. For intervals that are very short (5 to 50 μ sec)--less than one or two periods of the dominant frequencies in the echoes, the effects of overlap appear primarily as fluctuations in overall amplitude. (The spectral notches created by interference are

located at such widely-spaced frequencies that their existence as *notches* is obscured by the large amplitude changes they produce across the whole echo.) The echo components reinforce and cancel each other by as much as 5 to 6 dB. Such large changes in the amplitude of the composite echo redefine the task of detecting the test-echo component in the presence of the clutter; its presence is marked by interference-induced increases or decreases in the strength of the composite sound taken as a unit. In the two-choice task, the single clattering echo is paired with the dual test-plus-clutter echo, and the bat would encounter readily discriminable amplitude differences between these sounds for certain time separations (15 or 30 μ sec in Fig. 6, for example).

For time separations that are comparable to more than one or two periods of the echoes, the effects of overlap will appear primarily in terms of the location and spacing of spectral notches. (The notches are narrow enough and close enough together that their effects are restricted to small frequency regions and they are obvious as *notches*.) The overall amplitude of the sound remains about the same. In Fig. 6, for time separations between 100 and 600 μ sec, the interference between components manifests itself as amplitude modulations that appear more rapid as the time separation of the echo components becomes larger. These modulations are a reflection of the spectral notches in the time waveform. For even longer time separations, the two echo components will pull apart so that their individual waveforms will become directly distinguishable in delay.

The performance of the bats in the detection task is likely to reflect the shifting primacy of the acoustic cues shown in Fig. 6 as the interval between the test and cluttering echoes changes. The curve in Fig. 4 can be divided into three regions in terms of the available acoustic cues--(1) a narrow central region (within about 100 μ sec of the 3.27-msec delay assigned to the test echoes) where the combined test-plus-clutter echoes will fluctuate in overall amplitude according to the size of their time separation, (2) an intermediate region (time separations from about 100 to about 400 to 600 μ sec) where the amplitude of echoes will remain the same but spectral notches and amplitude modulations will change with their separation, and (3) an extended region (greater than about half the duration of the bat's emitted sounds) where the test and cluttering echoes will be separable in the raw echo waveform itself.

The fine structure shown in the clutter interference zone in Figs. 3 and 4 (large fluctuations in performance for small changes in time separation) is a consequence of interference between the test echo and the cluttering echo from the same loudspeaker when they are separated by intervals of less than a one or two periods of their average frequency. The relationship between overall echo amplitude and time separation has peaks at separations of zero, one, two, three,...periods, and valleys at separations of one-half, three halves, five halves,...of a period. The average period of the sonar signals of *Eptesicus* and also the echoes returned to the bats ears is about 30 μ sec. This period is the reciprocal of the average or dominant frequency of the first harmonic of the signals,

which is 30 to 35 kHz--see Fig. 5 (Simmons and Stein, 1980). The actual shape of this oscillatory pattern is obtained by crosscorrelating the two overlapping component waveforms. Fig. 7 shows the crosscorrelation function between two echoes plotted on the

INSERT FIG. 7 ABOUT HERE

same time scale as the detection performance of one of the bats in the clutter interference experiment (Bat 1 in Fig. 3). (The sonar sounds of all five bats have essentially the same autocorrelation function; that is, the heights of the peaks vary by no more than about 10% and the location of the first side-peak shifts by no more than 1 to 3 microseconds, so this example is adequate to represent the echoes received by any of the bats during the experiment. The signal used to compute the crosscorrelation function in Fig. 7 was recorded from bat 1, so this bat's performance is included in the figure. As Fig. 4 shows, the mean performance of all the bats has a similar fine structure to that of Bat 1.)

The waves of the crosscorrelation function in Fig. 7 mark the time separations where the sum of the test and cluttering echoes is greater (upward peaks) or smaller (downward peaks) than the clutter echo alone. If the bat takes advantage of the large amplitude fluctuations in the composite echo to distinguish the test-plus-clutter stimulus from the clutter-alone stimulus, its performance should be better for time separations near these peaks than between them. In Fig. 7, the bat indeed achieves better detection performance for those time separations of the test and cluttering echoes

that correspond to the central peak ($\Delta t = 0$) and first side-peaks ($\Delta t = \pm 30 \mu\text{sec}$) of the crosscorrelation function. In particular, when the amplitude of the composite echo containing both the test and cluttering echoes is larger than the amplitude of the cluttering echo alone (upward-going peaks), the bat in Fig. 7 performs better than when the two echoes add together to create a compound echo that has about the same or a weaker overall amplitude as the cluttering echo alone. In Fig. 3b, the performance of all the bats in the fine-structure region generally mirrors that of the bat in Fig. 7 (Bat 1), with the interesting exception that one bat (Bat 3) took advantage of the reversal in the relative amplitudes of the positive and negative stimuli at a separation of $-20 \mu\text{sec}$ to choose the wrong side on 80% of the trials. From Fig. 7, the reinforcement or cancellation of echo components is directly manifested in the bat's behavior. Under these conditions, clutter interference evidently constitutes simultaneous masking of one set of echoes by another, and the bats behave as though they perceive the test echo in terms of the large amplitude fluctuations caused by its mixing with the cluttering echo. It should be noted that the crosscorrelation function is invoked here merely to describe the effects of mixing two echo components to create a composite echo of variable overall amplitude (see Fig. 6), not to draw conclusions about the images of targets perceived by bats when the overlap of echoes is excluded by the use of a jittered-echo technique (Simmons, 1979).

Clutter interference is not restricted to the small time separations of the central region of acoustic cues. A strong clutter interference effect persists for time separations of the

test and cluttering echoes that exceed the small number of average periods associated with dramatic changes in overall echo amplitude. The crosscorrelation function in Fig. 7 has "settled down" to approximately its zero level for time separations of more than ± 70 μ sec, while the bats continue to experience depressed detection performance for time separations going beyond 70 μ sec to at least 200 to 300 μ sec (Fig. 4). Evidently clutter interference occurs for time separations where the degree of echo separation is reflected in the location and spacing of spectral notches or echo amplitude modulation (see Fig. 6) rather than in changes in overall echo amplitude. Over this intermediate acoustic region, the clutter interference effect declines precipitously as the separation between the test and cluttering echoes increases, until every trace is gone for separations larger than about 500 μ sec. In Fig. 6, the waveforms of the two echo components are still greatly overlapped, although the beginning and end of the overall waveform now starts to show them as separating. The extended region where the two components become truly distinct in time is not reached until their separation approaches half the duration of the bat's signals or 1 to 2 msec, but the effects of clutter interference have completely dissipated before the echoes are separated that much. Aside from the close relation between echo summation and the bat's performance in the central region (see Fig. 7), the shifting acoustic cues available to the bat from the raw echo waveforms are only loosely related to the strength of clutter interference for most separations. To better describe the acoustic basis for clutter interference, this analysis needs to be refined further by

taking into account the role of the inner ear in determining which cues are relevant to the bat.

The auditory representation of echoes: The first stage of auditory signal-processing that seriously modifies echo waveforms occurs when sounds pass through the parallel band-pass filters of the Organ of Corti prior to excitation of auditory-nerve fibers. The patterns of mechanical excitation created at any given site along the basilar membrane have different waveforms than the echo itself owing to the frequency selectivity of that site and its associated restriction of the FM sweep to a narrower frequency segment. The tuning properties of these peripheral auditory filters have not yet been adequately measured in *Eptesicus*, but they have been measured in the related species, *Myotis lucifugus* (Suga and Jen, 1977).

Myotis is an insectivorous bat in the same family as *Eptesicus* (Vespertilionidae). It emits FM sonar signals that are generally similar to those of *Eptesicus* (Griffin, 1958). Being smaller, the frequencies of its signals are somewhat higher. We can estimate the consequences of auditory filtering on the echoes received by *Eptesicus* if we use the data on tuning in *Myotis*.

The tuning curves of peripheral auditory neurons in *Myotis* have high-frequency skirts with a slope of about 260 to 290 dB/octave and low-frequency skirts with a slope of about 110 dB/octave (Suga and Jen, 1977). These filter properties are assumed here to reflect the selectivity of mechanical excitation delivered to individual hair cells driving auditory-nerve fibers. To illustrate the effects of peripheral auditory filtering on the sonar signals used by *Eptesicus*, a bank of 19 parallel elliptical

band-pass filters was synthesized in a computer, and sample *Eptesicus* sounds were digitally filtered using their coefficients. (No particular significance is attached to the use of elliptical filters; they merely are convenient to use, and they provide for minimal ripple in the filter pass-band.) The filters had frequency-response curves that approximated the tuning curves of auditory neurons in *Myotis*. Their center frequencies were distributed logarithmically from 24 to 96 kHz, and the equivalent sampling rate applied to the sounds passed through the filters was 400 kHz. The accuracy of the digital filtering process was limited to 12 bits, which corresponded to the accuracy with which the sounds were originally digitized.

Fig. 8 shows a spectrogram of one of the *Eptesicus* sounds used to study the effects of peripheral auditory filtering. It was emitted by Bat 4 (Fig. 5D) during one

INSERT FIG. 8 ABOUT HERE

trial of the detection experiment with clutter present, and it is representative of the vast majority of sounds emitted by most of the bats during these experiments. This particular signal has a duration of about 3.6 msec, which is near the modal duration used by the bats as a group, and it has an FM harmonic structure. Fig. 9 shows the output of the 19 model auditory filters with the *Eptesicus* signal from Fig. 8 used as input. The individual "auditory" filter responses are arranged in a spectrogram format with the

INSERT FIG. 9 ABOUT HERE

filter center frequencies on a logarithmic vertical axis. (The logarithmic frequency scale is a first approximation to the presumably nonlinear frequency scale actually used by the bat.) The original, unfiltered bat sound is shown as the top trace (*signal*). Each filter output represents mechanical excitation delivered to a particular site along the basilar membrane. The array of filter outputs closely resembles the spectrogram of the sound in Fig. 8 except for partial removal of the curved shape of the frequency sweeps by the logarithmic frequency scale of the auditory filters. Each filter yields a short burst as the signal sweeps through its response region. The bursts of "mechanical excitation" have durations of about 200 to 700 μ sec, depending primarily on the slope of the FM sweep in the region of the filter's center frequency. Filters tuned to frequencies near the end of the sound have longer output bursts because the sound dwells for a longer time in the filter's response area.

The filter outputs shown in Fig. 9 should be taken as crude approximations to the mechanical excitation delivered to hair cells at locations along the bat's Organ of Corti corresponding to the filter frequencies. They represent one version of the proximate stimuli associated with reception of echoes in the clutter interference experiment. Within each auditory frequency "channel," the excitation delivered to the hair cell evokes one or more nerve discharges from fibers innervating that particular receptor. The

filter outputs lead to a volley of on-discharges that represent the time-of-occurrence of the filter excitatory frequencies in the form of a neural spectrogram. At the inferior colliculus of FM bats, these on-discharges are especially prominent and seem clearly to register the shape of the FM sweeps of emissions and echoes (Bodenhamer and Pollak, 1981; Simmons and Kick, 1984). Two separate echoes would evoke two separate nerve discharges in each frequency channel as long as they are far enough apart that their bursts of mechanical excitation are able to separately stimulate the neurons. The term "channel" is used generically to mean the aggregate of neurons innervating a particular hair cell or site along the basilar membrane. If the echoes are close enough together that their excitation bursts run together, the volley of discharges normally evoked by the second echo would be absent, having been preempted by the first. The pattern of neural discharges evoked by two overlapping echoes would depend upon the time separation of the echo components in relation to the length of the bursts of mechanical activity that each component produces.

Figure 10 shows a series of mechanical-excitation spectrograms and their corresponding neural spectrograms or "neurograms" for the set of ten two-glint echoes already illustrated in Fig. 6. This is a schematic presentation of

INSERT FIG. 10 ABOUT HERE

the patterns of mechanical and neural activity associated with different time separations of the echo components. It is little

more than a cartoon, but it is intended to refine the analysis of the acoustic cues for detecting the test echoes in the presence of clutter to take into account the radical changes introduced into stimulus waveforms by the inner ear. The neural pattern shown for a single echo component (two perfectly superimposed echo components at $\Delta t = 0$; upper left in Fig. 10) is used as a baseline to interpret the patterns for all the other time separations. The solid dots show hypothetical neural on-discharges evoked in each frequency channel by the mechanical activity delivered through the basilar membrane.

For all time separations (Δt) larger than zero, the neural discharges evoked by a single echo component (two perfectly superimposed echo components) are shown as open dots to provide a frame of reference for reading the changes caused by the presence of two echo components separated to varying degrees.

Two kinds of changes related to time separation appear in Fig. 10: The amplitude of the mechanical excitation delivered through the band-pass filters changes as the time separation of the echo components moves the resulting spectral notches to different frequency regions. These are manifestations in the mechanical excitation of the amplitude modulations shown in Fig. 6. In addition, the mechanical excitation for time separations larger than about 200 μsec breaks into two separate bursts as the amount of separation starts to exceed the duration of the burst evoked by a single echo component (upper left). At 600 μsec (lower right), the bursts of excitation are completely separate even though the raw echo waveform still shows extensive overlap of the two echo

components. These changes in mechanical excitation are mirrored in the neurograms by changes in response latency and by the appearance of two separate neural discharges marking the individual echo components if they are far enough apart. In general, the time-of-occurrence of neural discharges depends upon stimulus amplitude, so the discharges shown in Fig. 10 are retarded (moved to the right) if the amplitude of the mechanical excitation in any particular channel is less than that for the single echo component. This increased response latency appears as the horizontal distance between the open and closed dots in each channel. For zero time separation, the neural spectrogram resembles a digitized version of the mechanical-excitation spectrogram, but, at greater time separations, the latency shifts distort the neural spectrograms considerably. The location of notches in the spectrum of the compound echo shows up in the neurograms as a displacement of the solid dots to the right, away from the relatively straightforward spectrogram indicated by the open dots. There is thus an odd-looking transformation of the amplitude of the mechanical-excitation bursts into a scalloped appearance of the neurograms, especially for time separations of 10 to 100 μsec . For larger time separations, where the envelope of the mechanical excitation clearly shows two maxima, a separate solid dot represents the neural discharge for each echo component.

From Fig. 10, the divergence of the overlapping echo components is large enough to evoke two separate neural discharges in each frequency channel at time separations of 400 and 600 μsec . At 200 μsec , the divergence is only partial, and just over half of the

channels have two discharges. The range of separations where a discrete neural representation identifies each echo component evidently falls between 200 and 400 μ sec in this example. This corresponds with the results of the clutter interference experiment in that the steeply-sloping sides of the clutter interference zone (Fig. 4) are located 200 to 400 μ sec away from the delay of the test echoes. If the analysis shown in Fig. 10 is a reasonable approximation to what happens in the inner ear of *Eptesicus*, the bat probably detects the test echoes if they are far enough away from the cluttering echoes to evoke a separate volley of discharges in auditory-nerve fibers. This occurs when the mechanical excitation evoked in the inner ear by each echo is separated into discrete bursts.

The shapes of the envelopes of the mechanical excitation bursts shown in Fig. 10 determine just how much separation must occur between echoes for them to be represented by separate bursts and thus separate neural discharges. If the mechanism outlined in Fig. 10 indeed is responsible for clutter interference, then the shape of the clutter interference zone itself should be related to the shape of these bursts. To examine this possibility, the envelopes of the excitation bursts from Fig. 9 were averaged to estimate the effect of peripheral auditory filtering on the FM signals received during the clutter interference experiment. The sonar signal shown in Figs. 8 and 9 is approximately the modal signal used by the bats in these experiments. From passing several representative signals of longer or shorter duration through the model filter system, this signal indeed is representative of the

proximate stimulation available to the bats. Fig. 11 shows the mean excitation envelope (plus or minus 1 standard deviation),

INSERT FIG. 11 ABOUT HERE

normalized and plotted on the same scale as the mean performance of the bats in the clutter interference experiment (Fig. 4). The behavioral data were fitted to the mean excitation envelope by setting chance performance (50 percent errors) equal to the envelope maximum, and detection performance in the absence of clutter (10 percent errors) equal to the envelope baseline of zero. This is crude but in keeping with the rough nature of the auditory model as a whole. To a first approximation, the clutter interference zone corresponds to the excitation envelope, which suggests that the collision of peripheral auditory excitation between the test and the clattering echoes creates clutter interference in a detection task.

Eptesicus apparently defines a discrete sonar target to be represented by the volley of nerve discharges evoked by its echoes. Two targets merge into one target when they become close enough together that the volley of discharges marking the second target disappears as a result of the disappearance of the distinction between the underlying excitation patterns. From the behavioral data in Fig. 4, the integration time of the auditory system of *Eptesicus fuscus* for sonar echoes appears to be between 0.2 and 0.4 msec. Fig. 11 indicates that this integration time may originate in the tuning of frequency channels in the auditory periphery and

may thus represent the windowing of FM sweeps in time by the selectivity of filters in frequency. More refined behavioral experiments with the echolocating porpoise, *Tursiops truncatus*, yield an estimate of about 260 μ sec for the integration time (Au, *et al.*, 1988), but this result has not been analyzed in auditory terms. The results shown in Fig. 11 suggest that the echo integration time in bats is a consequence of the filtering action of the Organ of Corti.

From the results of the clutter interference experiment, one might suppose that *Eptesicus* and other FM bats actually cannot distinguish between two objects that are nearer to each other in range than about 4 or 5 cm. In fact, *Eptesicus* performs in other kinds of experiments as though the true range-axis image of a point-target is less than a microsecond wide rather than a few hundred microseconds wide (Moss and Schnitzler, *in press*; Simmons, 1979; Simmons, *et al.*, 1974; see review in Simmons, 1987). The targets that bats can identify in airborne discrimination experiments have an acoustic structure that is entirely confined to the space within the clutter interference zone, yet the bats seem able to perceive this structure (Simmons and Chen, *in press*). The unusual organization of the bat's sonar receiver that enables acoustic images to contain sharp detail even within the clutter interference zone will be described in subsequent papers in the series that begins with this one.

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FIGURE CAPTIONS

Figure 1. A diagram of the two-alternative forced-choice procedure and the target simulator for investigating clutter interference and the integration time of the bat's sonar receiver. The bat is presented with electronically-returned echoes that simulate a test target (a) appearing on either the left or the right at a range of about 56 cm. If the bat moves forward towards this target (arrow), it is rewarded. Additional interfering echoes simulate cluttering targets (b_1 and b_2) located on both the left and the right at the same distance, either nearer or farther than the test target. The bat's sonar sounds are picked up by two microphones (m), delayed digitally to create the desired echo arrival-time at the bat's ears, and then returned from two loudspeakers (s). The experiment measures the bat's performance for detecting the test target in the presence of clutter at various distances around the position of the test target.

Figure 2. A graph of the frequency response of the left and right channels of the target simulator shown in Fig. 1. The sonar signals of *Eptesicus* contain energy from about 25 to 100 kHz (see Figs. 5 and 7), and the simulator returned the entire first harmonic (60 to 25 kHz) as well as most of the second harmonic up to about 80 to 85 kHz, but with emphasis on the first harmonic. Absolute calibration was checked daily and

maintained within a 3-dB range throughout the experiment (see text).

Figure 3. Graphs showing the detection performance (percent correct responses) for all five bats in the clutter interference experiment. In Graph a, the coarse-grain clutter data are plotted, with fine-grain clutter data for one bat (No. 1) included to fill in the curve. In Graph b, all the fine-grain clutter data are plotted to show the local fluctuations in performance in the region of the center of the clutter interference zone. Graph b is, in effect, a magnified segment of the coarse-grain plot in the region of the delay of the test echoes (arrow marked t on horizontal axes). Note that the bats all achieve good performance when the cluttering echoes coincide exactly with the test echoes, and that performance changes rapidly with echo delay in this central region.

Figure 4. Graphs showing the mean detection performance of the bats in the clutter interference experiment. The inset shows a magnified segment of the coarse-grain curve in the region of the delay of the test echoes (arrow marked t on horizontal axes). Note that the clutter interference zone as a whole is wider than the central region, with its local fluctuations in performance.

Figure 5. Spectrograms of six representative sonar sounds recorded from each of five *Eptesicus* during detection trials in the clutter interference experiment. These sounds had peak-to-peak amplitudes of about 100 dB SPL. Graphs A through E refer to Bats 1 through 5, respectively (see Fig. 3).

Figure 6. Waveforms of two overlapping echoes arriving with various delay separations (Δt) from zero to 600 μsec . The emitted signal is an *Eptesicus* sonar sound with a duration of about 2.5 msec (and with a shape shown for $\Delta t = 0$; upper left). The echoes are returned by glints having various separations in range. The waveforms show the effects of interference and cancellation of different frequencies along the FM sweeps in the echoes according to the amount of their time separation. The acoustic cues available for detecting the test echoes in the presence of clutter change as the time separation increases (see text).

Figure 7. A graph showing the central region of the performance curve (*Bat*) for Bat 1 in Fig. 3 superimposed on the crosscorrelation function (*XCor*) between a typical sonar emission and an echo recorded during the experiment (see text). The local fluctuations in detection performance follow the wave structure of the crosscorrelation function, suggesting that they represent the bat's use of overall echo amplitude variations to detect the test echoes when they reinforce or cancel the cluttering echoes. These amplitude variations diminish as the time separation of the echoes increases (see Fig. 6) and the spacing of spectral notches becomes small enough to place more than one notch along the frequency span of the echoes.

Figure 8. Spectrogram of a 3.6-msec FM sonar sound recorded from *Eptesicus* during the experiment and used to estimate the peripheral excitation evoked by echoes in the inner ear. This

is a prototypical approach- or tracking-stage (Kick and Simmons, 1984) signal emitted by *Eptesicus* during pursuit of flying insects (see Simmons, 1987, Fig. 2).

Figure 9. Waveforms depicting the output of 19 band-pass filters (approximating the tuning characteristics of peripheral auditory neurons in FM bats--see text) whose input is the FM signal shown in Fig. 8. The unfiltered sound appears in the top trace (*signal*). These waveforms are crude representations of the mechanical excitation delivered to sites along the Organ of Corti tuned to the indicated frequencies. The filter center frequencies are displayed along a logarithmic frequency scale to reconstruct the auditory system's spectrogram-like peripheral representation of the sound. These bursts of mechanical excitation evoke neural discharges in auditory-nerve fibers innervating hair cells at the different sites.

Figure 10. A schematic diagram of inner-ear mechanical excitation patterns and their associated auditory-nerve on-discharges ("neurograms") for the series of overlapping double echoes shown in Fig. 6. The 19-channel model filters from Fig. 9 were used to approximate mechanical excitation, and the neural data are derived from Bodenhamer and Pollak, 1981. The whole echo waveform appears in the top trace of each example. The response to a single echo ($\Delta t = 0$) provides a baseline for understanding how the time separation of the overlapping echoes alters the responses of the inner ear and auditory nerve (see text). Solid dots show neural responses to each stimulus and open dots show neural responses to a single echo

for comparison with responses to the different double echoes. Decreasing echo amplitude at certain frequencies reflects the placement of spectral interference notches according to the time separation of the overlapping components. Regions of decreased amplitude (relative to the amplitude for the single echo at $\Delta t = 0$) in the mechanical excitation bursts are transformed into increased neural response latency at those same frequencies. There is thus a kind of map of the echo spectrum in the neural latencies across different frequencies. The appearance of double volleys of neural discharges for time separations between 200 and 400 μsec is fairly well-matched to the size of the clutter interference zone in Fig. 4.

Figure 11. A graph comparing the mean detection performance for *Eptesicus* (percent errors) in the clutter interference experiment with the mean (plus and minus 1 standard deviation) envelope for the filter outputs shown in Fig. 9. The output envelopes are weighted by the frequency response of the simulator system (Fig. 2) prior to averaging. The fine structure of the central region of the clutter interference zone is omitted because it originates in reinforcement and cancellation of echo waveforms only at the very top of the performance curve. The similarity of the curves suggests that clutter interference originates in the mixing of mechanical excitation evoked by two echoes when their time separation is shorter than the duration of the excitation bursts.

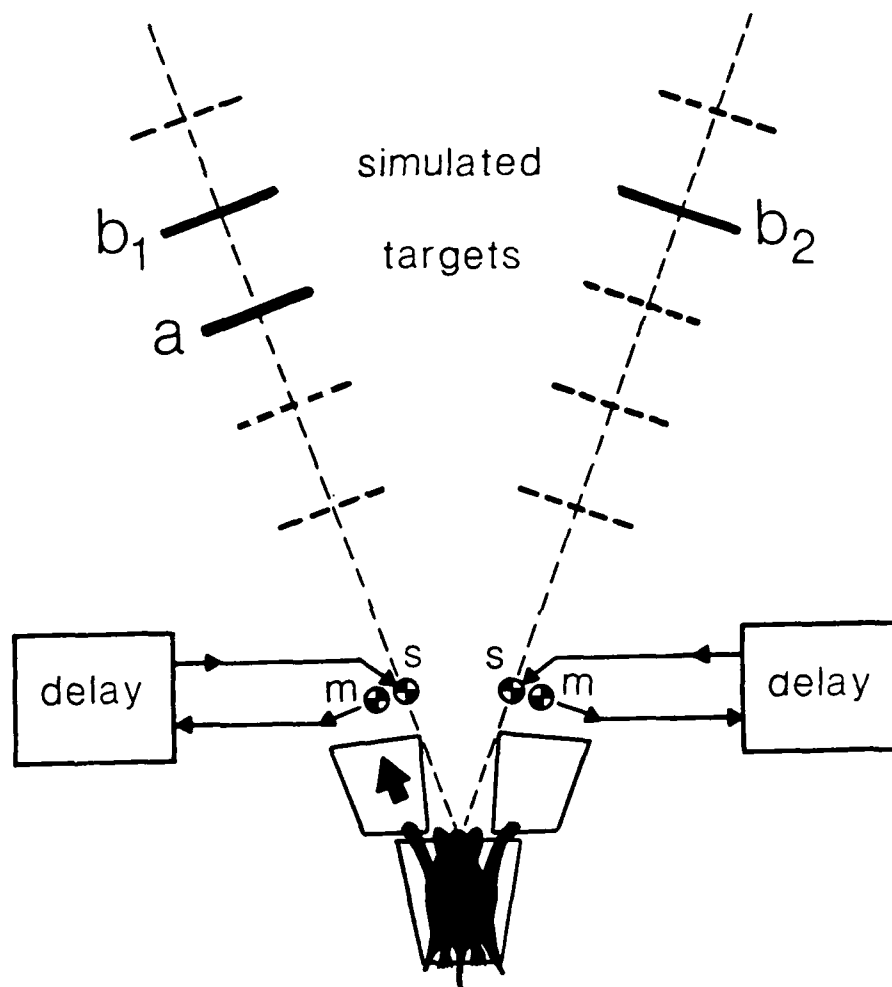


Figure 1

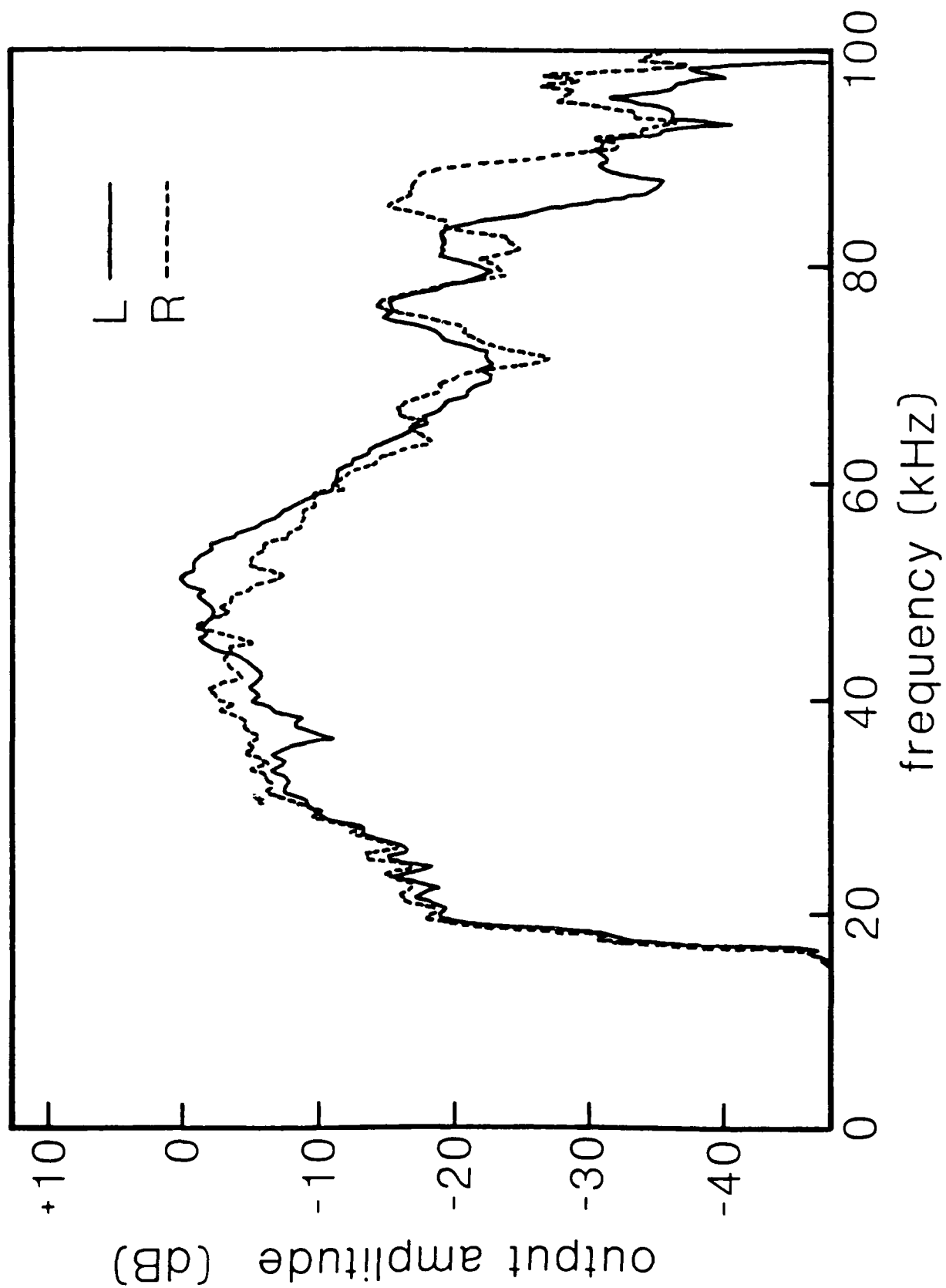


Figure 2

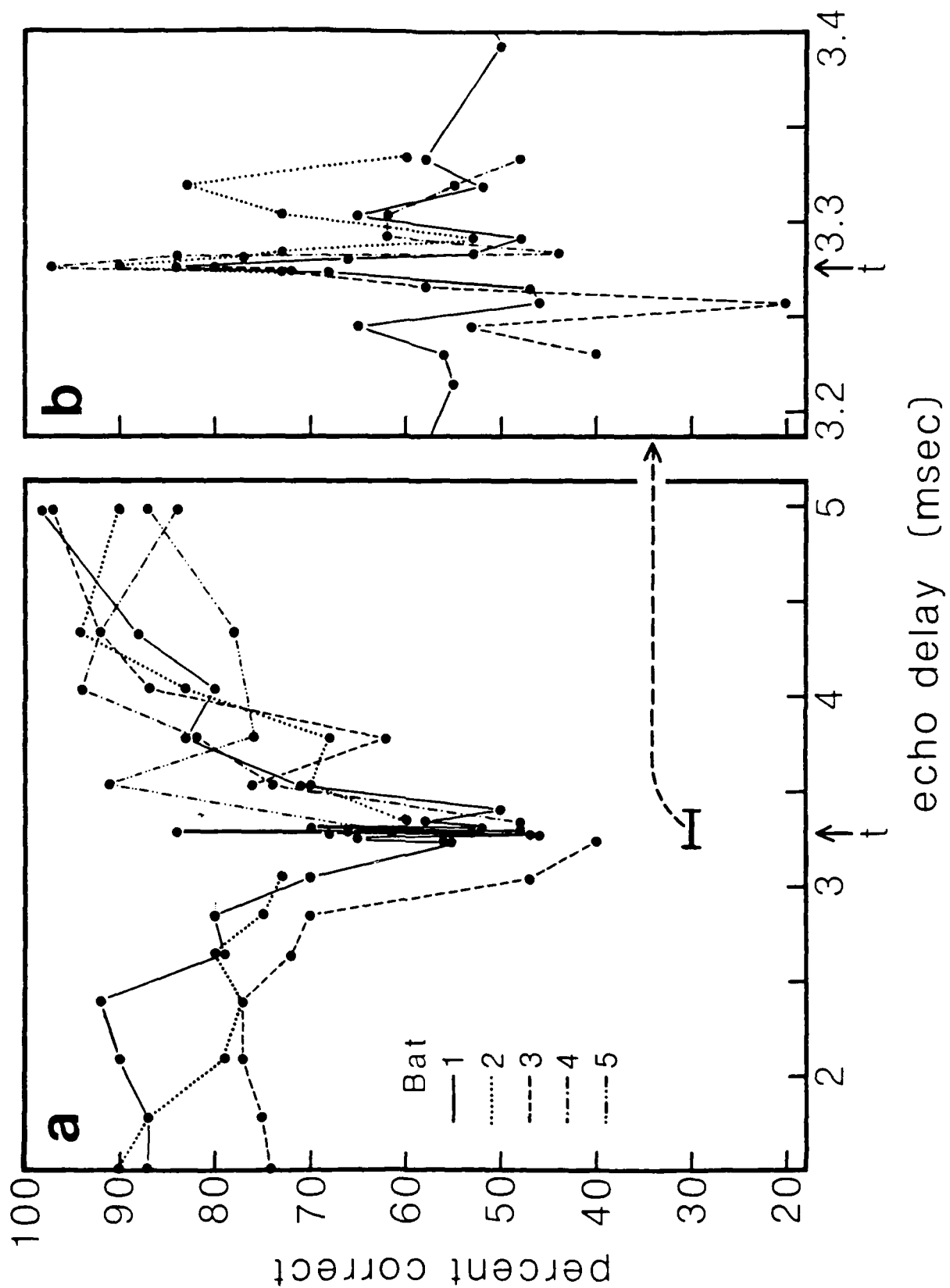


Figure 3

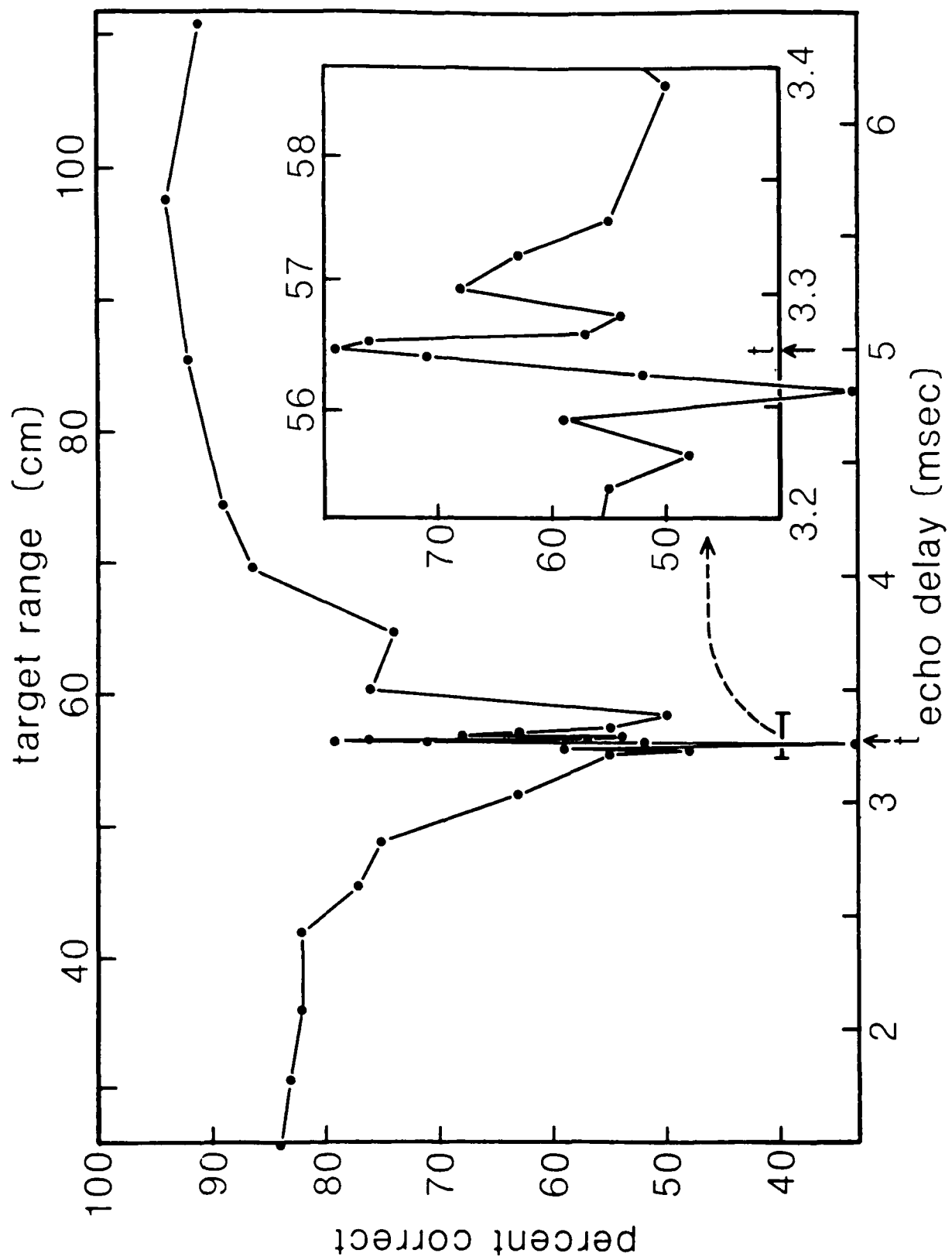


Figure 4

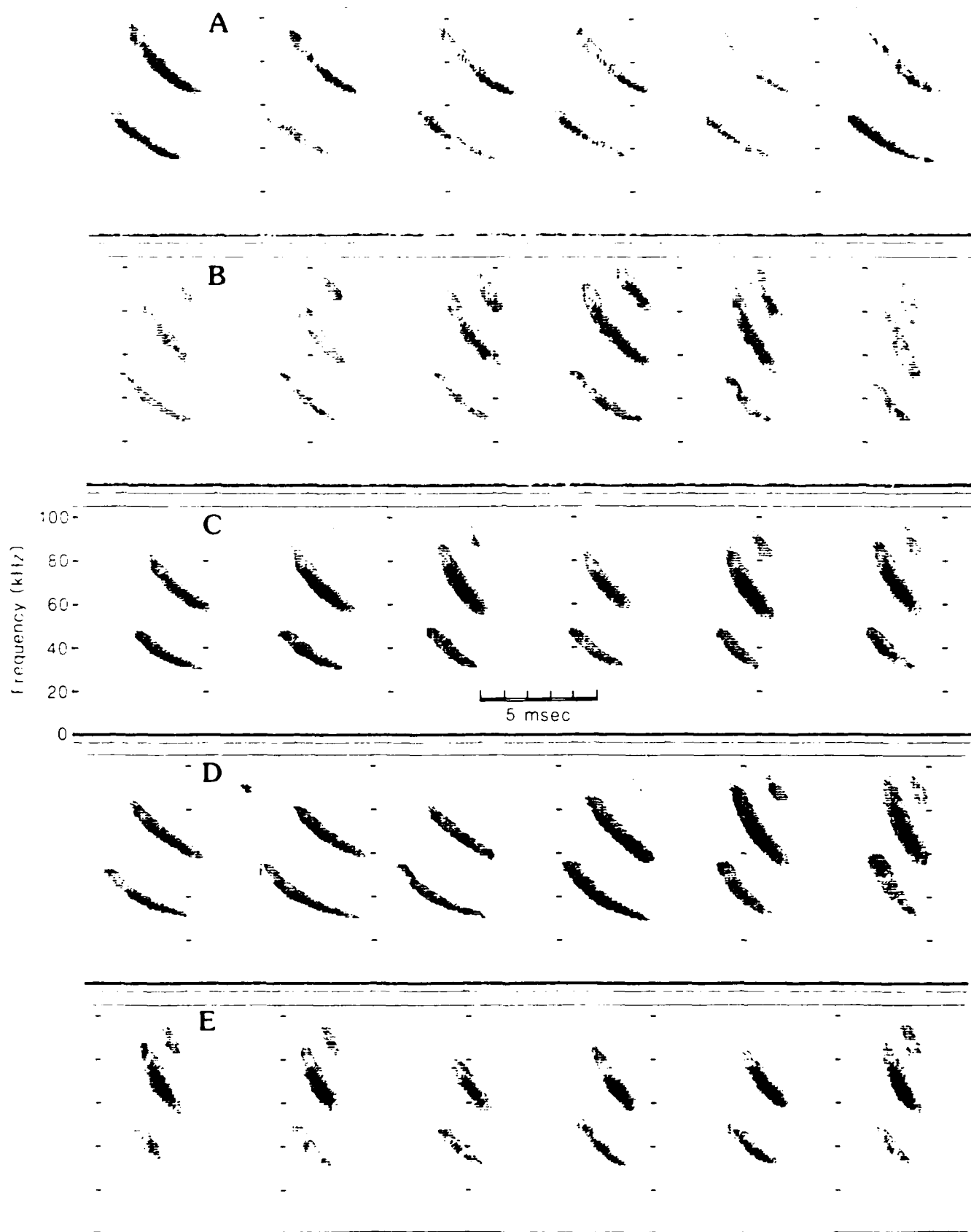
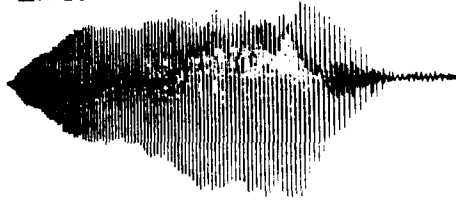


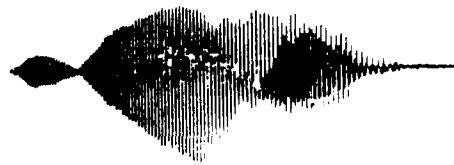
Figure 5

TWO-GLINT ECHOES

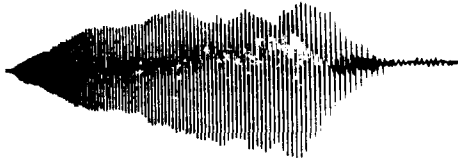
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Δt : 50 μ sec



Δt : 5 μ sec



Δt : 100 μ sec



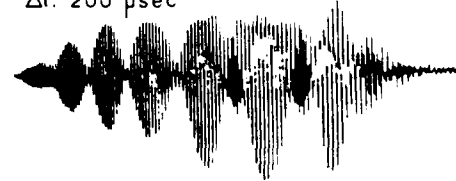
1 msec



Δt : 10 μ sec



Δt : 200 μ sec



Δt : 15 μ sec



Δt : 400 μ sec



Δt : 30 μ sec



Δt : 600 μ sec

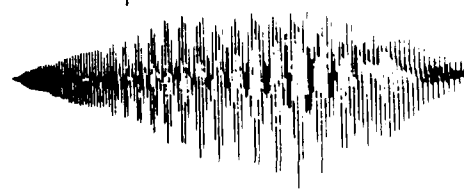


Figure 6

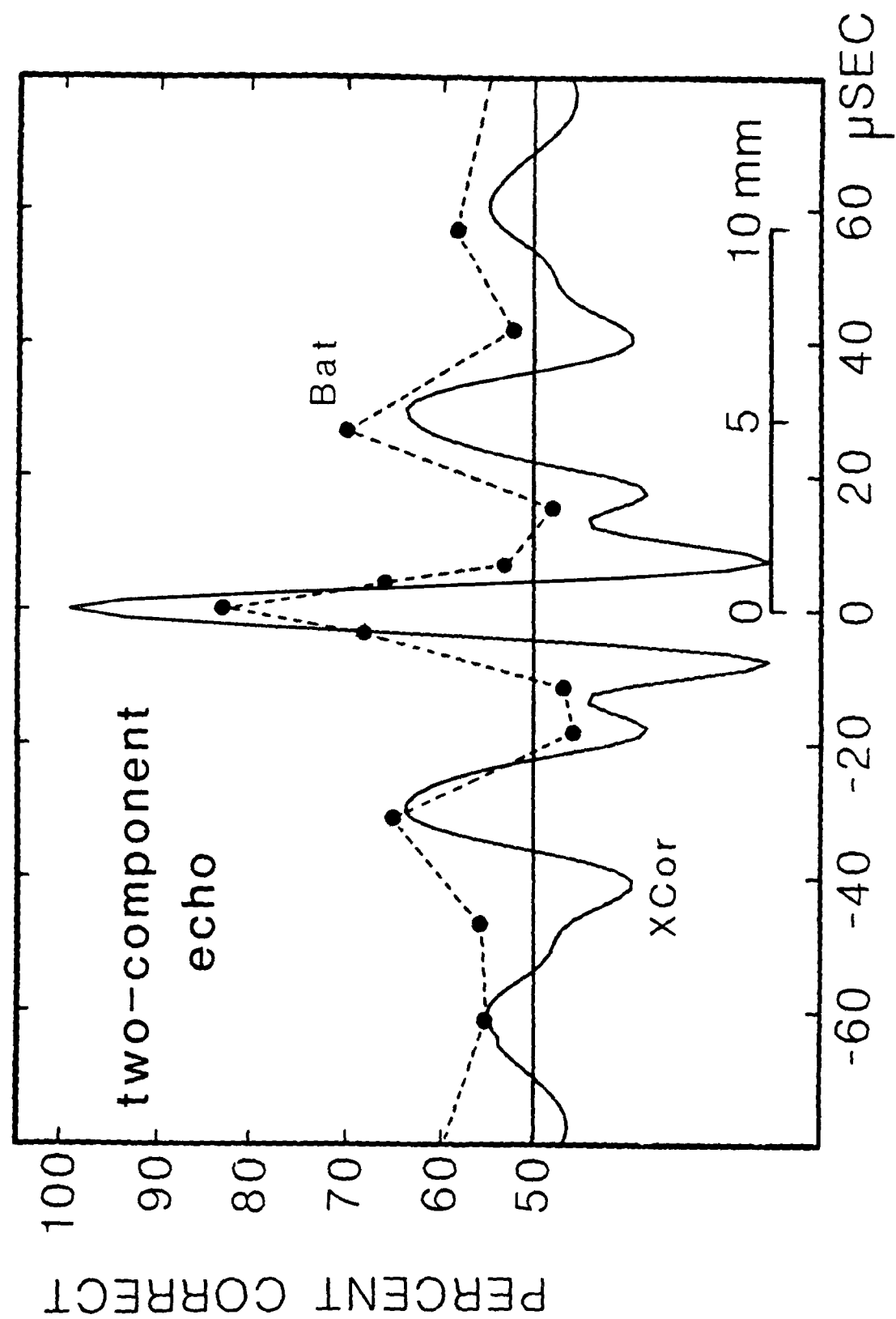


Figure 7

ECHO DELAY/TARGET RANGE

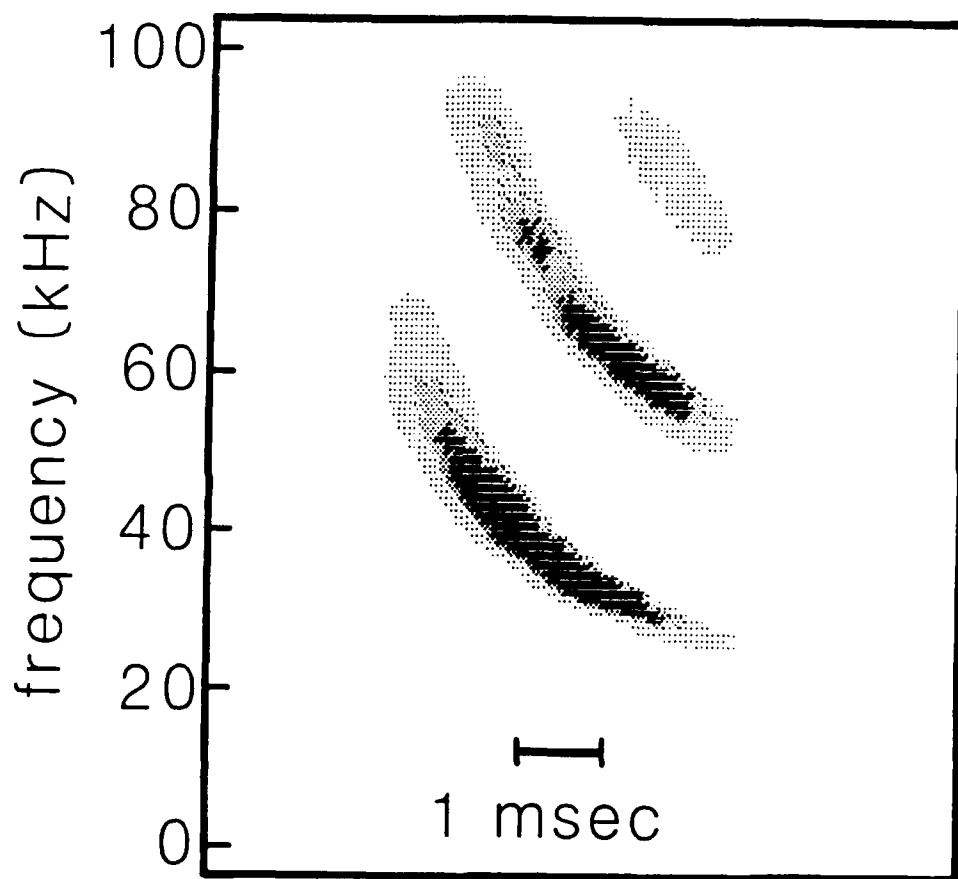


Figure 8

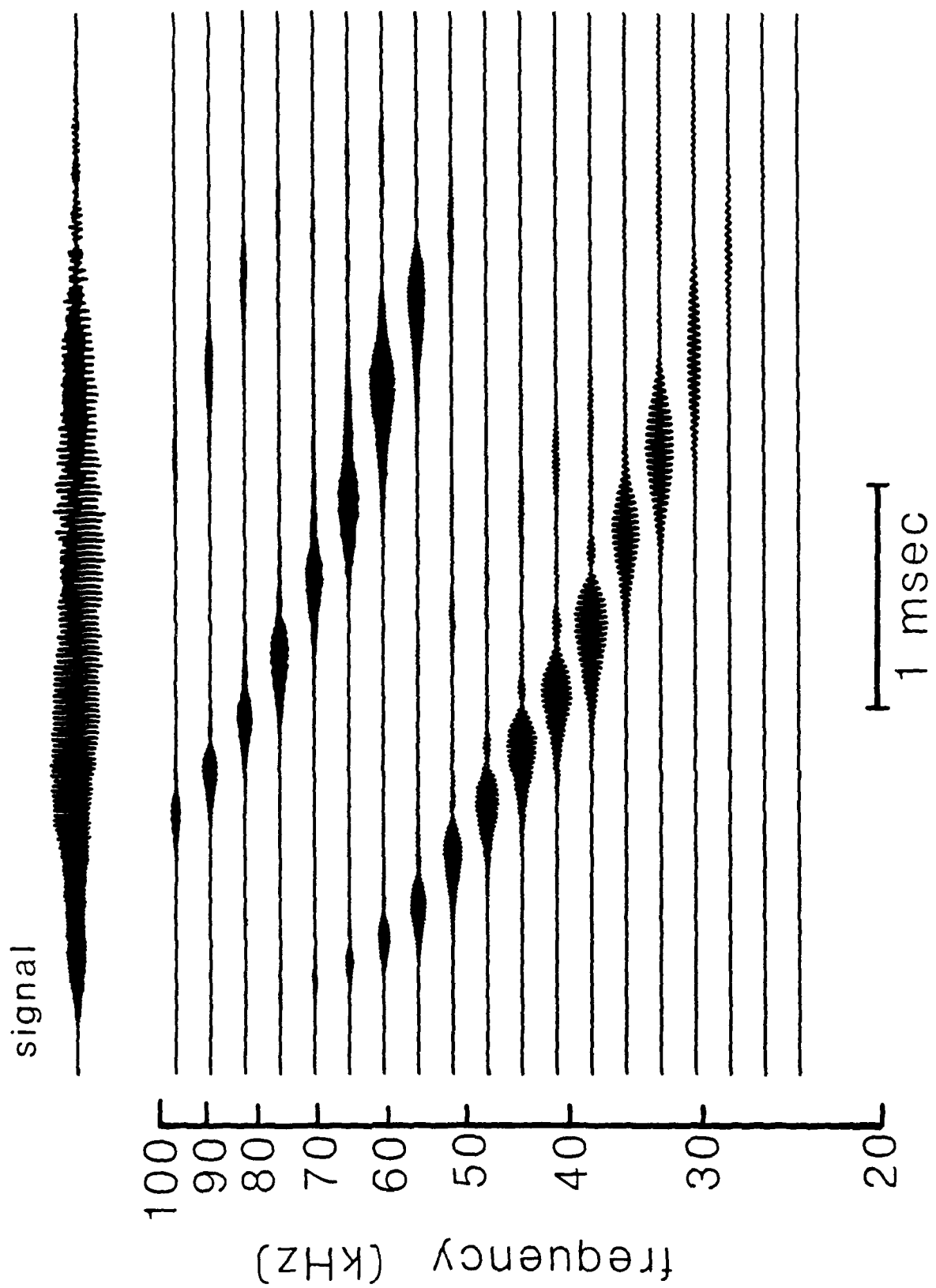


Figure 9

TWO-GLINT NEUROGRAMS

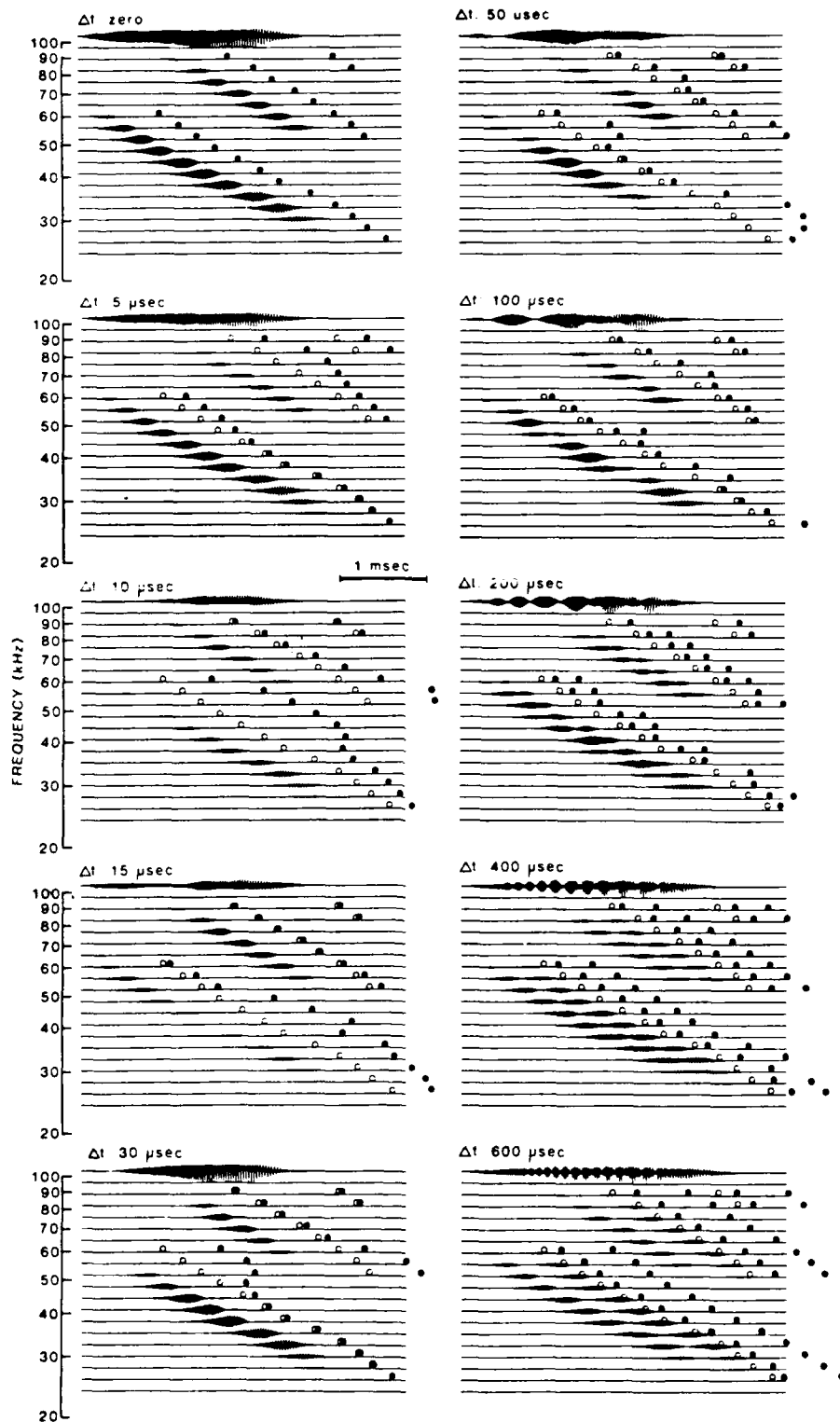


Figure 10

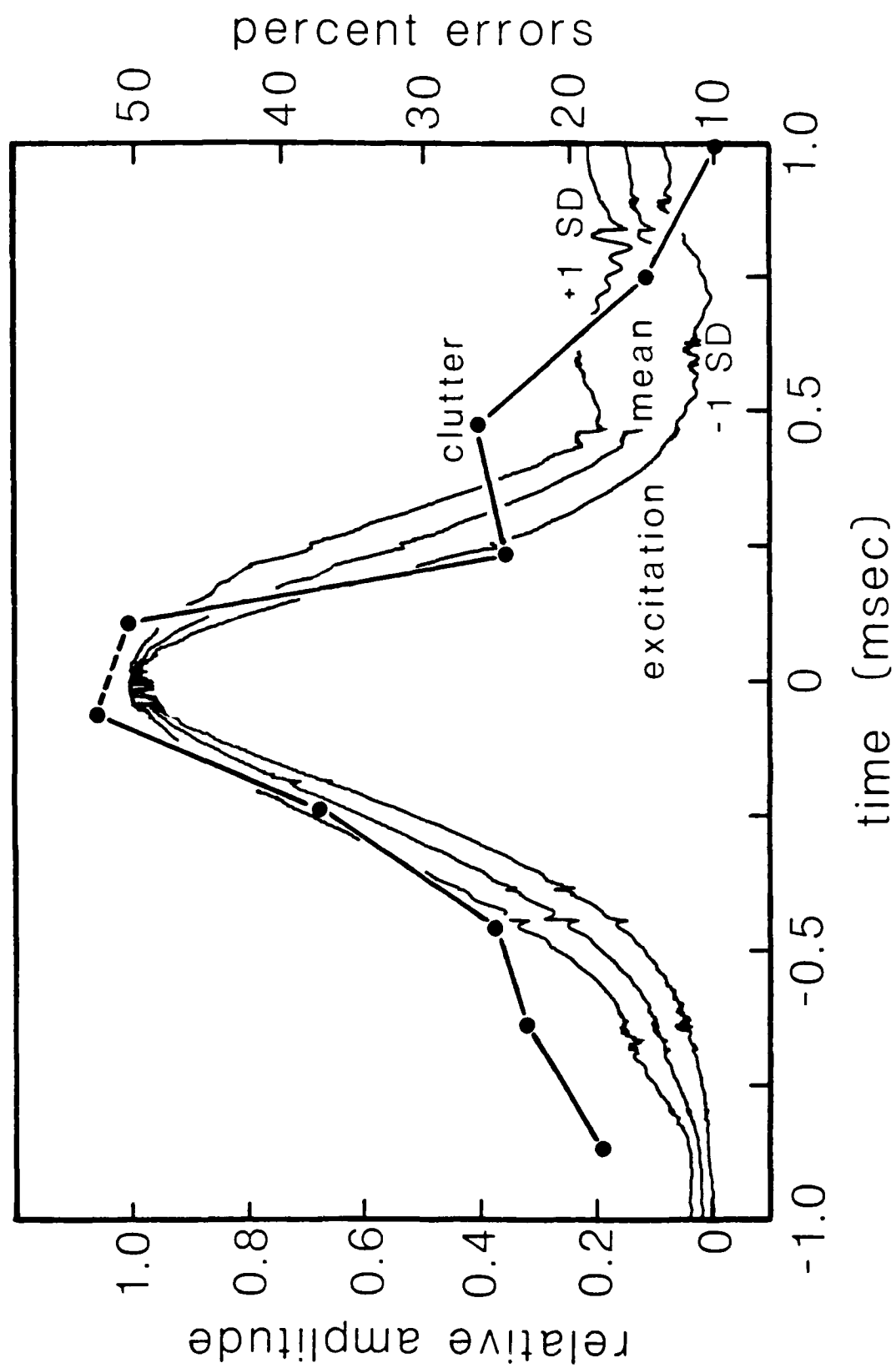


Figure 11

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